Primate feeding ecology: an integrative approach

MARTHA M. ROBBINS AND GOTTFRIED HOHMANN

No biologist would argue that ecology, "the scientific study of the interactions that determine the distribution and abundance of organisms," is not a complex topic. Feeding ecology is a central component of a species' biology, relating to its survival, reproduction, population dynamics, habitat requirements, and patterns of sociality. If one wants to best understand certain ecological processes, primates would not necessarily come to mind as the best organisms to study because of their long life-span and slow reproductive rates, the difficulties of getting sufficient sample sizes for statistical analysis, and the constraints on using wild primates for experiments. However, studying the feeding ecology of primates has been a major area of focus in primatological studies since field studies began because of the wide diversity of ecological niches occupied by primates, the heavy influence that ecology exerts on social behavior, and how it aids us in studying human evolution and behavior. Despite being a relatively small order, primates occupy a wide range of habitats and exhibit a huge diversity of grouping patterns and behavior. Studies of primate feeding ecology assist us in answering two main questions: Why do primates have the diets they do? Why do primates behave as they do? The aim of this book is to attempt to show the relationships among many of the aspects of the biology of primates to their environment.

Over the last four decades, there have been an ever-increasing number of field studies on apes and other primates that have focused on food acquisition, food processing, habitat utilization, foraging strategies, the relationship between ecology and sociality, and related topics. These studies have revealed that feeding ecology of apes and other primates is extremely diverse and complex. Perhaps more questions have been raised than answered concerning the relationship between feeding ecology and other variables such as habitat

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utilization and patterns of sociality. Additionally, newly developed techniques for laboratory analyses of primate foods are providing valuable tools that can be applied to answer questions on a finer scale than previously possible. To best understand the impact that feeding ecology has had on the evolution of the diversity of social systems that are observed in primates today, as well as human evolution, it is particularly useful to take an integrative approach and produce a synthetic volume that addresses these topics.

Organizational models of primate feeding ecology

To assist in orienting the reader to the topics discussed in this book, we present two frameworks in which to consider primate feeding ecology. First, we present a schematic model that shows the relationships and feedback among (A) the environment in which a primate lives, (B) the primate itself, and (C) the responses made by the primate to the environment, as constrained by the primate's morphology and physiology (Figure 1). The majority of primate ecology studies test hypotheses involving the relationship among at least two of these elements. Paradoxically, the primate itself may be the most difficult of these three elements to understand because what goes on internally in a primate is effectively a 'black box' due to the limits of invasive research on wild primates. The diet of a primate largely depends on the relationship between A and B. A primate can choose foods available in the environment and consume them within the limits of its ability to find them and process them (cognitively, manually, and digestively). A primate may in turn influence its environment through seed dispersal or how it influences the evolution of plant defences against consumption.

The relationship between A and C is the focus of the majority of primate behavioral ecology research. For example, patterns of diet, ranging, and habitat utilization are formed by food availability, within the constraints of a species' body size, digestive abilities, and abilities to detect and process foods (B). The socioecological model, which drives the majority of research on the social behavior of primates, rests on the assumption that the distribution and abundance of food resources has a strong influence on the type of relationships exhibited by female primates (Wrangham, 1980; van Schaik, 1989; Sterck *et al.*, 1997; Isbell & Young, 2002). Additionally, food availability will influence the density of primates that an area can support as well as modulate the population dynamics (e.g., Chapman *et al.*, 2004, Marshall & Leighton, Chapter 12, this volume). Conversely, the density of primates will determine the amount of food resources depleted from the environment.

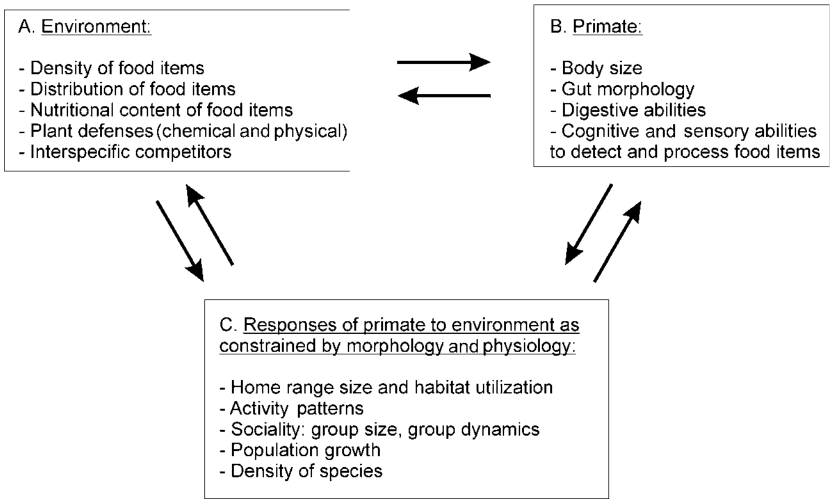

Figure 1. A schematic model of the relationships among a primate, its environment, and the responses of a primate to its environment.

Second, in an attempt to categorize complexity of the biological world, ecologists typically organize things according to a hierarchy or different levels of systems, specifically ecosystems, landscapes, communities, populations, and organisms (Goss-Custard & Sutherland, 1997; Barrett & Peles, 1999). In the case of social animals such as primates it is particularly important to insert ‘social groups’ in between populations and organisms. Interestingly, in the introductory chapter to the classic book on primate feeding ecology, Clutton-Brock stressed that it is the first volume to focus on social groups and not on population level processes (Clutton-Brock, 1977). Nearly 30 years later, this appears almost odd given that in recent decades the majority of primate field studies focus on social groups, because of the ecological influences on primate sociality. Primate feeding ecology is examined on the level of the organism, particularly when studying the relationship between the nutritional content and defenses of food resources and a species’ food processing abilities. Populations of primates are the focus of research, particularly when addressing questions concerning what influences the density and distribution of primate populations, but such studies are often difficult to carry out because of the work involved in generating sufficient data on entire populations (longitudinally and/or cross-sectionally) and other variables such as food resources. Studying primates on the community level is most difficult because it involves studying the interactions of multiple species with their environment, but the topic has recently been the focus of a synthetic study in the book *Primate Communities* (Fleagle *et al.*, 1999).

A particularly important concept to keep in mind when studying ecology is the issue of scale (Brown *et al.*, 1995). For example, consider the difficulties of attempting to quantify the diet of a species. First there is the temporal scale. Not only is there likely to be daily and seasonal variation, but also variability between years. Second, there is spatial scale. Most primate studies are restricted to the study of only 1–2 social groups because of the logistical and financial constraints of habituating and monitoring more groups. Field observations of howler monkeys that were transferred to new habitats showed that individuals were able to adapt quickly to novel food sources (Silver & Marsh, 2003; see also Visalberghi *et al.*, 2003). These studies suggest that individuals tolerate major shifts in their overall diet composition. Meanwhile, an increasing number of studies are showing that there is remarkable variation in the diet of primate species, sometimes even among neighboring groups (Byrne *et al.*, 1993; Koenig & Borries, 2001; Chapman *et al.*, 2002; Ganas *et al.*, 2004; see also Boesch *et al.*, Chapter 7, this volume). Finally, at what level do we want to quantify the diet? According to the proportion of the diet in volume that consists of each type of plant part (e.g., fruit, seed, pith, leaves, etc.), of each species of plant consumed, time spent feeding on each resource, of each macronutrient (e.g., protein, sugars, etc.), or of total caloric intake? The scale at which a study is conducted is likely to be determined by the specific questions and hypotheses researchers are addressing, but also may be limited by the abilities of researchers to collect data (e.g., limited study period). However, a complete picture of primate feeding ecology will require looking ‘upward’ towards population and community level processes as well as looking ‘inward’ toward particular processes such as the nutritional composition of plants and digestive abilities of primates.

Understanding primate diet

The motivation of researchers to investigate the diet of a given primate species varies. Sometimes, data are obtained as a by-product of research on other topics. The value of this type of information is that it offers a bench mark against which data from other studies can be compared. For example, for a long time colobines were regarded as folivores (Davis & Oates, 1994). Equipped with a multichambered stomach, they seemed to be perfectly adapted to a diet dominated by leaves. Recent field studies made clear that colobines are seed-eaters that turn to leaves as fall-back food during times when other foods are in short supply (Koenig & Borries, 2001). In addition, to further our understanding of the intra-specific variability of dietary breadth, accounts of food lists have turned out to be a rich source of information for post-hoc comparison. Using information from a large number of field studies on great apes, Rodman (2002) analysed how the different species of African and Asian apes use the plant food sources available to them. The results of his study suggest that observed differences in food selection between the taxa reflect patterns of forest composition rather than preferences for certain subsets of plant food species. The integrative work by Rodman offers a unique source of information and has a large potential to expand in different ways. In addition, it highlights the significance of two parameters that are often neglected by primatologists, plant taxonomy and plant species diversity.

Primate diets appear to be complex in structure, diverse in content, and variable over time. Consequently, understanding a species' diet requires different perspectives. Identification of the nature of selected food items appears relatively easy but is complicated by the question of why individuals select a given food out of an almost uncountable number of potential resources. Depending on the dominant type of food, species have been classified as being frugivore, insectivore, or folivore. While this terminology has its legitimacy, it does not account for the traits that characterize diet selection by primates. Almost all primates exploit a large variety of different resources including fruit, seeds, leaves, flowers, bark, gum, insects, and meat and unlike many other omnivore vertebrates the diet of most primates combines a broad spectrum of plant foods with a narrow spectrum of animal food (Milton, 1987). There are different models explaining the intake of mixed diets (Westoby, 1978a; Freeland & Janzen, 1974a; for a review see Singer & Bernays, 2003) but so far few studies have applied the predictions to primates (e.g., Altmann, 1998). Given the wide spectrum of food items, primates are considered as being food-generalists (e.g., Harding, 1981). However, unlike other vertebrates that exploit the same sources, primates tend to process food dentally, manually, or technically (Boesch & Boesch, 1981; Taylor, 2002; Lambert *et al*., 2003). Thus, food selected is not necessarily equal with food ingested and in spite of its potential significance in terms of nutrition, physical alteration of food items by primates has deserved surprisingly little attention.

"Hidden and consequently neglected keys to unlocking the mystery of why animals eat what they do is how food is processed after ingestion" (Levey & Martinez del Rio, 2001). While this quotation comes from a review on avian nutritional ecology, it applies equally well to primates. There is a rich literature on the content of macronutrients and anti-feedants of food items. However, what really matters in the context of nutrition is what individuals are able to extract from the ingested food. The efficiency of assimilation of nutrients depends, amongst others, on the time that food needs to pass through the digestive system (Lambert, 1998). Differences in food passage time are related to chemical and structural features of the food (Milton, 1981). From this, one may infer that information on dietary quality may provide considerable insight into the digestive strategy of the species in question. Findings from other mammals indicate a causal relationship between a species body size and diet (van Soest, 1996). Thus, in theory, data on body mass should predict dietary quality which, in turn, should allow us assign to the digestive strategy. Evidence suggests that primates violate the predictions of both models: For example, in spite of their large body size, chimpanzees consume a diet that is superior to the one eaten by sympatric Cercopithecines (Wrangham *et al*., 1998). Another example is the unusually fast passage time of some medium-sized primates that appears to be related to the anatomy of certain parts of the digestive system rather than dietary quality (Milton, 1981; Lambert, 1998; see also Janson & Vogel, Chapter 11, this volume). While the studies cited above have advanced our understanding of the relationship between environment, food selection, and digestion, primate nutritional ecology is still in an early stage. Understanding dietary selection means to understand one of the most basic interactions between individuals and their environment: resource acquisition, and the external and internal processing of these resources. While previous studies have taught us much about how primates search, find, and compete for food, the modes of physical and physiological deployment of food sources are still largely unknown.

Understanding primate behavior

A major focus of primate field studies is the relationship between food availability, diet, movement patterns, and sociality. Three decades ago, Tim Clutton-Brock (1977) compiled a book on a number of comparative primate studies. Unlike earlier publications, the chapters of the book applied the same set of questions to a wide range of species including lemurs, monkeys, and apes. The book also contained some of the first attempts to test hypotheses that would show general trends in primate ranging and grouping patterns. For example, Clutton-Brock & Harvey (1977) showed the positive relationship between body size and home range size, which has stood the test of time and more modern statistical analysis (Nunn & Barton, 2000). Additionally, the prediction that as group size increases, the amount of food needed collectively by the group also increases, and daily travel distance and home range size should expand accordingly has been broadly supported and emphasizes the ecological constraints on group size (Clutton-Brock & Harvey, 1977; Janson & Goldsmith, 1995; Altmann, 1998; Chapman & Chapman, 2000). Various other aspects of movement patterns of primates have received considerable attention in the recent edited volume *On the Move* (Boinski & Garber, 2000). Understanding the cognitive abilities used by primates to locate food sources and to forage efficiently is a complex topic to tackle, but an increasing number of studies are elegantly addressing the issue (Boesch & Boesch, 1984; Byrne, 2000; Janson, 2000).

Interest in primate feeding ecology has been driven largely by questioning the adaptive significance of the highly variable social systems observed in primates. The major principle of the socioecological model is that the distribution, density, and quality of food resources will have an impact on the competitive interactions observed among female group members of diurnal primates, which in turn will influence the type of female social relationships exhibited (Wrangham, 1980; van Schaik, 1989; Sterck *et al*., 1997; Koenig, 2002; Isbell & Young, 2002). In brief, the distribution and abundance of food resources will determine the strength of competitive interactions for access to food resources (e.g., if individuals exhibit scramble or contest competition), the structure of dominance relationships (e.g., despotic vs. egalitarian), the benefits derived from associating with kin (e.g., alliance formation), and female dispersal patterns. Testing the socioecological model has focused on comparing related species that vary in both ecological conditions and relevant traits (e.g., Barton *et al*., 1996; Boinski *et al*., 2002).

Without any doubt, the incorporation of socioecological theories into primate studies has significantly advanced our understanding of the function of primate social systems and social relationships within and between groups. However, like other theories, socioecological models are not unchallenged and several studies have identified some important constraints of current theories (e.g., Isbell & Young, 2002; Koenig & Borries, Chapter 10, this volume). For example, conventional models associate folivory with widely distributed food sources of relatively low quality and, as a consequence, predict that folivores do not gain by competing for access to resources. Field studies on common langurs in Nepal revealed that the leaves of major food sources are patchily distributed and of high nutritional quality. Consequently, female langurs gain by competing for access to these resources, leading to significant skews in food intake (Koenig *et al*., 1998). More detailed studies of the nutritional value and distribution of food resources as well as behavioral studies of less-known species and populations of primates will provide further tests of the socioecological model, but we also need additional research that shows the link between social status, food intake, and fitness. To date, relatively few studies have shown a positive relationship between dominance rank, which is assumed to cause improved access to food resources, and female reproductive success, and even these are not able to show that reproductive success equals fitness (Pusey *et al*., 1997; van Noordwijk & van Schaik, 1999; Altmann & Alberts, 2003).

Lastly, another link between feeding behavior and sociality is that of cultural variation in food processing (Whiten *et al*., 1999; Fox *et al*., 2000; van Schaik & Knott, 2001; Panger *et al*., 2002) and even diet (Boesch *et al*., this volume). Van Schaik *et al*. (1999) proposed a number of conditions that promote the evolution of tool use: extractive foraging, manual dexterity, intelligence, social tolerance. The complexity of cultural variations is thought to depend on opportunities for social learning, and social tolerance is seen as the key for the transmission of inventions. Data from chimpanzees, orangutans, and gorillas are consistent with this hypothesis (Byrne & Byrne, 1993; Boesch *et al*., 1994; McGrew *et al*., 1997; van Schaik, 2002).

Future directions

Perhaps one of the major things we have learned over the past decades about primate feeding ecology is that it is incredibly complex. We encourage researchers to take an integrative approach in the field, in the laboratory, and in the theoretician's armchair. While researchers strive to create elegant, parsimonious theoretical models to explain particular systems and drive future research, additional data from the field typically muddy the waters. However, field data are necessary to test the robustness of model assumptions and they should be used to create refinements to existing models, refute them, and/or lead to the creation of new models altogether. For example, the chapters by Koenig *et al*. and Janson and Vogel in this volume offer useful refinements to the socioecological model and, it is hoped, will stimulate additional research on other species. Comparative studies using similar methodologies, both of the same species in different habitats and different, closely related species in the same habitat, provide useful tests in the absence of experimental studies (Barton *et al*., 1996; Sterk & Steenbeck, 1997; Pruetz & Isbell, 2000; Boinski *et al*., 2002; Danish *et al*., Chapter 18, this volume). Computer modeling could also be used to test predictions for which obtaining sufficient empirical data is difficult, for example examining the relationship between food availability, habitat utilization, and population dynamics.

Data collection needs to be expanded in all directions: more study sites, more long-term data, more detailed analysis of diet through nutritional analysis, etc. The key to understanding why primates eat the food they eat is hidden in the physical and chemical properties of food items on one hand, and the sensory skills and digestive strategies of primates on the other. Birds are perhaps the most important food competitors of primates and therefore, primatologists may benefit from looking at the findings from studies of avian nutritional ecology. Inter-specific differences in the ability to digest macronutrients, association patterns of secondary compounds, and differences in digestive anatomy are dimensions that have advanced the understanding of feeding ecology of birds but have been largely ignored in primate studies.

On a practical level, as an increasing number of primate species face extinction it is imperative to use research to assist with their conservation. Research should be focused to serve the dual purposes of answering questions relevant to understanding the evolution of primate feeding ecology and to conserving primates intact in their natural habitats. Studies of diet, ranging patterns, and habitat utilization are useful for understanding the habitat requirements to maintain viable populations and may also contribute to our comprehension of the population dynamics and carrying capacity of a particular area. Understanding the role that primates play in their community ecology as predators, prey, competitors, seed dispersers, etc. may assist in the conservation of entire ecosystems. As the habitats of primates shrink and become increasingly surrounded by human settlement, primates may be forced into marginal habitat and/or resort to crop raiding (Marsh, 2003). Knowledge of the dietary patterns of primates may assist in designing management strategies to reduce human–wildlife conflict. Studies of primate feeding ecology have revealed a great deal of flexibility in ecological patterns. While this knowledge of the variability may be used as an argument to conserve as many populations of a particular species as possible, conservationists also need to be aware that results from one population may not be appropriate for extrapolation to other populations of the same species. Only through concerted efforts of conservation and research will we be able to understand and appreciate the complexity of primates in their natural environments.

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